THE DISTRIBUTION OF THE DINOFLAGELLATE *WETZELIELLA* IN THE PALAEOGENE OF NORTH-WESTERN EUROPE

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ABSTRACT. The stratigraphical distribution of *Wetzeliella* in England, Belgium, and north Germany is reviewed. A very similar succession of species in these areas permits the establishment of eight *Wetzeliella* zones ranging from the late Upper Palaeocene to the Oligocene. Correlation based on *Wetzeliella* in north-west Europe is in agreement with that founded on calcareous nannoplankton. The zonation proposed for north-west Europe can be made to correspond with similarly based schemes established for the Upper Palaeocene–Lower Eocene of the southern Pyrénées (north-east Spain) and for the Palaeogene of the Alpine flysch (east France). In the Systematic Appendix, a new subgenus: *W.* (*Apectodinium*) and two new species: *W.* (*Apectodinium*) *paniculata* and *W.* (*W.*) *gochtii*, are introduced.

THE genus *Wetzeliella* Eisenack is one of the most characteristic and better-known elements in Palaeogene dinoflagellate assemblages. Since it was erected by Eisenack in 1938 this genus has received the attention of several investigators (Gocht 1955, 1967, 1969; Williams and Downie 1966; Wilson 1967; Vozzhennikova 1967), who considerably added to the knowledge on the morphology and taxonomy of the group. The relatively large number of works on Palaeogene microplankton assemblages published in the last decade has yielded abundant additional information on the distribution of many species in this genus. The stratigraphical range of *Wetzeliella* is relatively restricted: no species properly referable to this genus is known from sediments older than the Upper Palaeocene and it now seems certain that the genus becomes extinct in the Miocene. Of the thirty or so species of *Wetzeliella* described, the great majority occur in the Lower–Middle Eocene, the number decreases markedly towards the Oligocene and only one species (*W.* (*W.*) *symmetrica*) seems to occur in the Miocene. The picture offered by the group is that of a sudden and widespread first appearance in the late Upper Palaeocene, quickly followed by a rapid diversification which reached its maximum in the late Lower Eocene, and a progressive decline towards the Oligocene.

Wetzeliella has an extensive geographical distribution comprising eastern and western Europe, central Asia, New Zealand, Australia, and North America. Only one species has so far been recorded in South America and no records are known from Africa, the remainder of Asia, or the Antarctic. The most important centre of evolution and diversification for the genus appears to be western Europe, where the greatest number of species has been recorded. Australia and New Zealand appear to be other centres of evolution with endemic species, but the number of taxa and of published records is here much lower than in western Europe.

The first reference to the importance of *Wetzeliella* in Palaeogene biostratigraphy was made by Wilson (1967) who studied its distribution in the Palaeocene–Eocene of New Zealand. But it is only recently that the usefulness of members of this genus

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as stratigraphical indicators in Europe gained recognition. Russian workers have included *Wetzeliella* in the analysis of Eocene and Oligocene deposits in Ukraine, Crimea, and Tadjikistan (Grigorovich 1969, 1971; Grigorovich and Vyesyelov 1973; Olyenik 1973). Downie *et al.* (1971) proposed the '*Wetzeliella* phase' to characterize the Oldhaven and Woolwich Beds in south-east England and to apply this to correlation with the Belgian Landenian. The first zonal scheme based on *Wetzeliella* was introduced by Caro (1973) for the Upper Palaeocene–Lower Eocene of the southern Pyrénées in north-east Spain. In a work on the palynology, calcareous nannoplankton, and stratigraphy of the Alpine flysch in Haute Savoie (east France), Jan du Chêne *et al.* (1976, in press) also give special attention to the distribution of *Wetzeliella* in their zonation.

This paper is part of a more extensive reappraisal of the genus *Wetzeliella* in which the morphology, taxonomy, and evolution of this group have been reviewed. The establishment of a zonation scheme is based on an examination of the morphology and evolution in the different lineages distinguished within the genus, a detailed account of which will be presented in a separate paper. The systematics of *Wetzeliella* need some readjustments, the necessary changes are formalized in the Systematic Appendix at the end of this paper, this also includes a list of the taxa mentioned in the text.

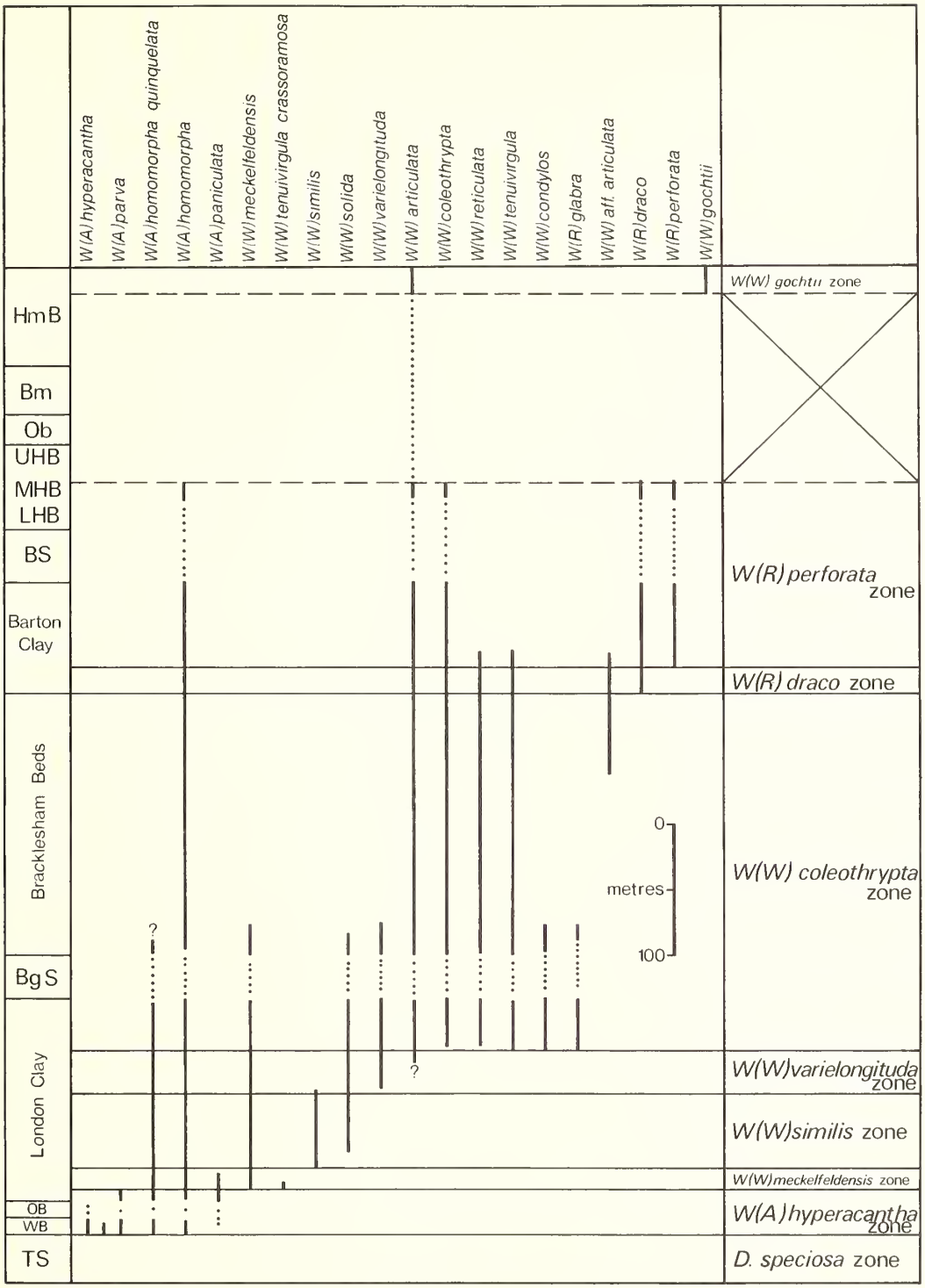
MATERIAL

The abundant British material employed for this work comprises several stratigraphical sequences ranging from the Upper Palaeocene to the Middle Oligocene, developed in the London and Hampshire basins, both in the south-east of England. The microplankton assemblages from these sections have already been studied by several workers (Williams, unpublished thesis, Sheffield 1963; Williams and Downie 1966; Husain, unpublished thesis, Sheffield 1967; Eaton 1971; Downie *et al.* 1971; Bujak, unpublished thesis, Sheffield 1973; Liengjarern, unpublished thesis, Sheffield 1973) and zonal schemes based on dinoflagellates have been proposed for the main sections.

A series of borehole samples from Meckelfeld (near Hamburg, north Germany) was made available by Professor E. Martini and Dr. P. Benedek (Frankfurt) who are currently studying the nannoplankton and microplankton content of the same. Dr. H. Gocht (Tübingen) made available material from his work on two Meckelfeld boreholes (1969); part of Eisenack's type material collection was also examined. Additionally, Dr. J. De Coninck (Gent) provided samples from the boreholes of Kallo, Merelbeke, and Sint Jan (Belgium). Photographs and valuable information about the species of *Wetzeliella* in the Alpine flysch were made available by Dr. R. Jan du Chêne (Geneva).

THE HISTORY OF *WETZELIELLA* IN SOUTH-EAST ENGLAND

The first occurrence of *Wetzeliella* in England is in the Woolwich Beds (Upper Palaeocene) (text-fig. 1) where there is a massive incoming of individuals belonging to the species *Wetzeliella* (*Apectodinium*) *homomorpha* subsp. *quinquelata*, *W.* (*A.*) *homomorpha* subsp. *homomorpha*, *W.* (*A.*) *parva*, and *W.* (*A.*) *hyperacantha* (Pl. 92,



TEXT-FIG. 1. The range of selected *Wetzeliella* spp. in England. TS, Thanet Sands, WB, Woolwich Beds; OB, Oldhaven Beds; BgS, Bagshot Sands; BS, Barton Sands; LHB, Lower Headon Beds; MHB, Middle Headon Beds; UHB, Upper Headon Beds; Ob, Osborne Beds; Bm, Bembridge Marl; HmB, Hamstead Beds.

fig. 6), the first being, by far, the most abundant. The *Wetzeliella* species in the Woolwich Beds are closely interrelated, the discrimination between them often being difficult due to the continuous variation in the critical morphological characters and the abundance of intermediate forms. These taxa conform to a clearly distinct group within the genus and they are accorded here the status of a separate subgenus: *Wetzeliella* (*Apectodinium*). The species involved differ from other *Wetzeliella* species by lacking a clearly separate endoblast (the endophragm being closely appressed to the periphragm) and, consequently, a distinct pericoel. The association of *Wetzeliella* species in the Woolwich Beds constitute the '*Wetzeliella* phase' of Downie *et al.* (1971) and completely dominates the microplankton assemblages.

In the lower part of the London Clay, a new species, *W.* (*A.*) *paniculata* (Pl. 92, fig. 1) becomes quite abundant. Two species substantially different from those mentioned above, *W.* (*W.*) *meckelfeldensis* and *W.* (*W.*) *tenuivirgula* subsp. *crassoramosa* first occur a few metres above the base of the London Clay in both the London and the Hampshire basins. These species, with a subrhombic outline, four well-developed horns, and a well-differentiated and usually thick-walled endoblast, are easily distinguished from *W.* (*A.*) *homomorpha* and *W.* (*A.*) *paniculata* which also abound in these assemblages. Two taxa from the beds below, *W.* (*A.*) *parva* and *W.* (*A.*) *hyperacantha*, apparently disappear at this point. *W.* (*W.*) *similis*, a species presumably derived from *W.* (*W.*) *meckelfeldensis*, is first recorded in the London Clay a few metres above the first appearance of this latter. The appearance of *W.* (*W.*) *similis* at Whitecliff Bay (Isle of Wight) coincides with the planktonic foraminifera datum recognized by Wright (1972) in this section, this datum is marked by the incoming of a number of planktonic foraminifera species not recorded earlier. *W.* (*W.*) *solida*, originating from *W.* (*W.*) *similis*, appears shortly above this horizon and becomes progressively more abundant until it almost completely replaces *W.* (*W.*) *similis* in the assemblages. *W.* (*A.*) *paniculata* becomes very rare and disappears in this part of the section. *W.* (*A.*) *homomorpha* is still abundant, particularly at Alum Bay. *W.* (*W.*) *meckelfeldensis* is also present although it is rare. The next stage in the succession of species of *Wetzeliella* in the London Clay is marked by the appearance of *W.* (*W.*) *varielongituda*, probably derived from *W.* (*W.*) *solida* or *W.* (*W.*) *similis*, near the top of the London Clay at Whitecliff Bay and about 80 m above the base of the London Clay at Herne Bay. *W.* (*W.*) *solida*, *W.* (*W.*) *meckelfeldensis*, *W.* (*W.*) *lunaris*, and *W.* (*A.*) *homomorpha* are also present in these assemblages.

A remarkable increase in the diversity of this genus is registered approximately 35 m below the top of the London Clay at Sheppey, with the incoming of a number of species such as *W.* (*W.*) *coleothrypta*, *W.* (*W.*) *tenuivirgula*, *W.* (*W.*) *articulata*, *W.* (*W.*) *reticulata*, *W.* (*Rhombodinium*) *glabra*, and *W.* (*W.*) *condylos*. All the species occurring immediately below this horizon persist into these assemblages, although some of them (e.g. *W.* (*W.*) *solida* and *W.* (*W.*) *meckelfeldensis*) are very rare. *W.* (*A.*) *homomorpha homomorpha* is now dominant over the subspecies *quinquelata*. The only section of the London Clay where this assemblage is represented is that at Sheppey (Kent), but it also occurs at the bottom of the Bracklesham Beds in the Isle of Wight. The microplankton assemblages in the lowermost Bracklesham Beds (Bed I of the section at Whitecliff Bay, Fisher 1862) contain almost the same *Wetzeliella* species as those at the top of the London Clay at Sheppey, although in less abundance.

Above this bed, the number of species of *Wetzeliella* decreases considerably. *W.* (*R.*) *glabra*, *W.* (*W.*) *solida*, and *W.* (*W.*) *varielongituda* apparently do not occur above this bed; *W.* (*A.*) *homomorpha* subsp. *quinquelata* occurs only occasionally in the Bracklesham Beds, the subgenus being now represented almost exclusively by *W.* (*A.*) *homomorpha* subsp. *homomorpha* which is very abundant in some horizons of the section at Alum Bay. The diversity of *Wetzeliella* is further diminished above the beds with *Nummulites variolarius* and *N. laevigatus* (Fisher's Bed VIII) where *W.* (*W.*) *condylos* and *W.* (*W.*) *meckelfeldensis* seem to disappear. The composition of the assemblages in so far as *Wetzeliella* is concerned is very uniform in the remainder of the Bracklesham Beds and no new species of the genus appears in the sequence. *W.* (*W.*) *articulata* and *W.* (*W.*) *coleothrypta* occur throughout the Bracklesham Beds and may be very abundant in some horizons. Although the *Wetzeliella* assemblages vary very little throughout this sequence, considerable intraspecific variation is observed in *W.* (*W.*) *articulata* and also, although less pronounced, in *W.* (*W.*) *coleothrypta*. This variability seems to be, at least in part, due to environmental control and similar varieties may not occur elsewhere. However, a distinction of varieties of *W.* (*W.*) *articulata* may possibly prove a useful element to apply in correlation, at least within the Hampshire Basin. In the Upper Bracklesham Beds (Fisher's Beds XI–XIX) the forms listed here as *W.* (*W.*) aff. *articulata* (Pl. 92, fig. 4) become very abundant; similar forms are found in the Bournemouth Marine Beds and the Hengistbury Head Beds, as well as in the Lower Barton Clays.

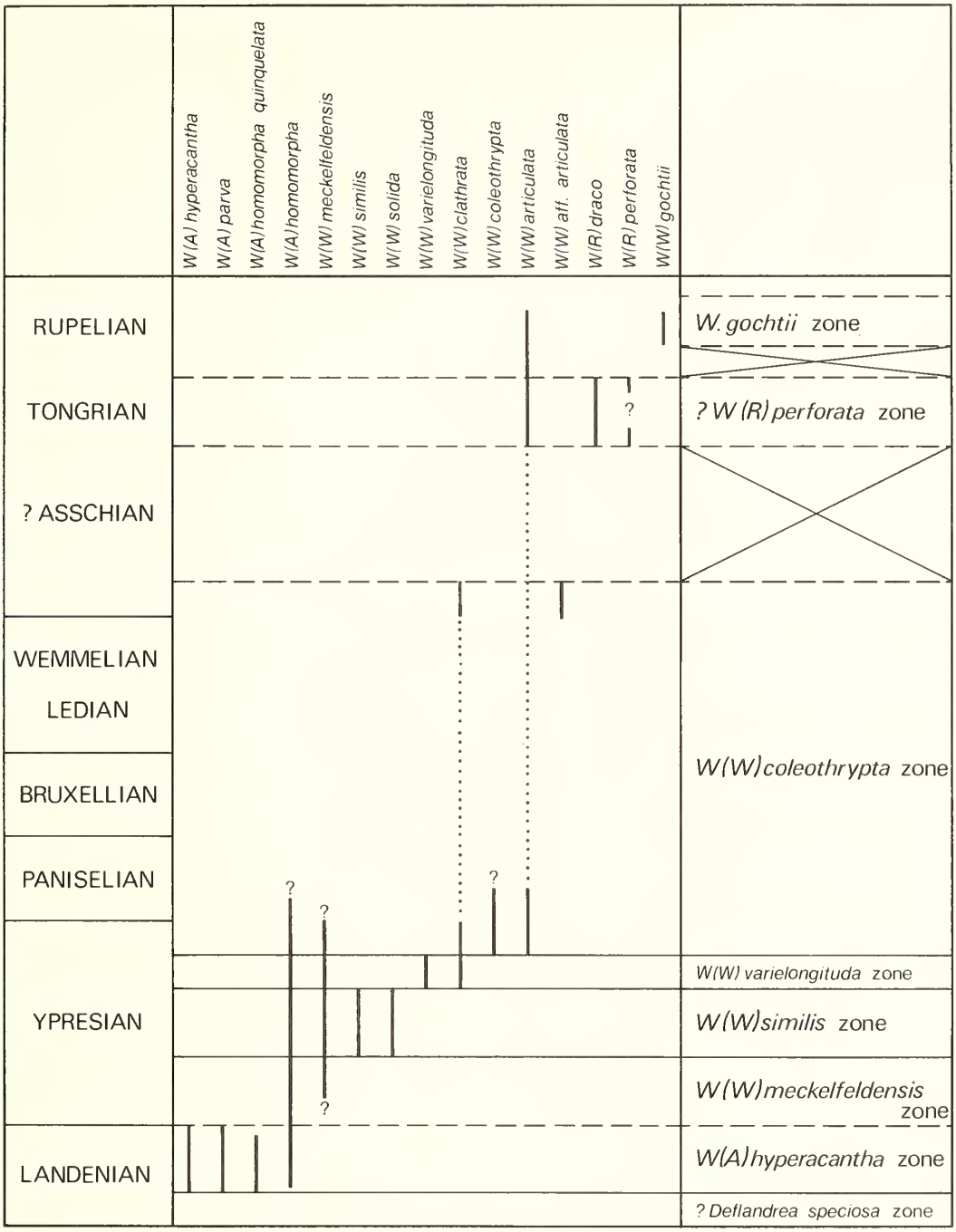
The base of the Barton Clays, marked by the *N. prestwichianus* Bed, registers the first appearance of *W.* (*R.*) *draco*, this species is, in fact, one of the very few elements in the microplankton assemblages that enables a distinction to be made between the top of the Bracklesham Bed (Fisher's Beds XVII–XIX), dinoflagellate zone 5 of Eaton, unpublished thesis, Sheffield 1969) and the base of the Barton Clays. The forms of *W.* (*R.*) *draco* in the Barton Clays are considerably smaller than the German type material for the species, but they are identical to this in all remaining characters. About 25 m above the base of the Barton Clays at Highcliffe, *W.* (*R.*) *perforata* (Pl. 92, fig. 5) is first recorded. This species presumably derives from *W.* (*R.*) *draco*, which it resembles in most characters (including size) and from which it is distinguished by the strongly perforated periphragm. Also in the Middle Barton Beds, an unpublished species of Bujak (thesis, Sheffield 1973) which is apparently related, if not synonymous, to *W.* (*W.*) *symmetrica* makes its first appearance, persisting up to the top of the Barton Clays. Apart from those already mentioned, other species recorded in this sequence are: *W.* (*W.*) *coleothrypta*, *W.* (*W.*) *articulata*, *W.* (*W.*) *reticulata*, *W.* (*A.*) *homomorpha* subsp. *homomorpha*, and *W.* (*R.*) *longimanum*. The succession of *Wetzeliella* species is interrupted above the *Chama squamosa* Beds of the Bartonian, and the next records of the genus are found in the Middle Headon Beds with *W.* (*W.*) *coleothrypta*, *W.* (*W.*) *articulata*, *W.* (*A.*) *homomorpha*, *W.* (*R.*) *draco*, *W.* (*R.*) *longimanum*, and *W.* (*R.*) *perforata*. The succession is again interrupted above these beds, dinoflagellates being very scarce, when not absent, in the overlying Upper Headon Beds, Osborne Beds, and Bembridge Beds, as well as in the Lower Hamstead Beds. The only species of *Wetzeliella* in the Upper Hamstead Beds are *W.* (*W.*) *articulata* and *W.* (*W.*) *gochtii* n. sp. (Pl. 92, figs. 2–3), which are the last representatives of the genus recorded in England.

THE DISTRIBUTION OF *WETZELIELLA* IN BELGIUM

De Coninck's works on the microplankton of the Belgian Ypresian (1965, 1968, 1972) enable a precise correlation between this and the Upper Palaeocene–Lower Eocene of south-east England. Only the distribution of *Wetzeliella* has been taken into account in the present work, but it appears most likely that a similar appraisal of the whole of the dinoflagellate assemblages in both areas would provide further support to the correlation proposed on text-fig. 4. Additional information on the distribution of *Wetzeliella* is provided by Rozen (1965), Morgenroth (1966), and Weyns (1970).

As can be seen on text-fig. 2, the succession of species of *Wetzeliella* in the sections studied by De Coninck is practically identical to that observed in the Woolwich Beds–London Clay–Lower Bracklesham Beds in south-east England (text-fig. 1). The typical assemblages of the Woolwich Beds are clearly identifiable in the Sables d'Ostende-ter-Streep (Landenian 2) which also lithologically resemble the Woolwich Beds. As *Wetzeliella* sp., De Coninck (1968, p. 21) includes *W.* (*A.*) *homomorpha homomorpha* (his pl. III, figs. 13–14, 17–18, 20), *W.* (*A.*) *h. quinquelata* (his pl. III, figs. 7–12, 15–16, 19) and, according to the description given by the author (p. 21), also *W.* (*A.*) *hyperacantha*. *W.* (*W.*) *meckelfeldensis* appears shortly above the base of the Argile d'Ypres (figured as *W.* aff. *symmetrica* in De Coninck 1968, pl. IV, fig. 9). As in the London Clay, *W.* (*W.*) *similis*, immediately followed by *W.* (*W.*) *solida*, appears a short distance above the first occurrence of *W.* (*W.*) *meckelfeldensis*, and *W.* (*W.*) *varielongituda* is first recorded about 70 m above the base of the Argile d'Ypres.

W. (*W.*) *coleothrypta* has not been recorded by De Coninck, but the species has now been found in a position corresponding to that in the London Clay at Sheppey. It should be pointed out that this species is easily confused with *W.* (*W.*) *clathrata*, to which it is very closely related, and it is sometimes difficult, particularly in unstained material, to tell one from the other. Also in the Upper Ypresian of Belgium, Morgenroth (1966) recorded *W.* (*R.*) *glabra*, as well as the species recorded by De Coninck. The Paniselian (P1) in the Kallo borehole appears to contain microplankton assemblages resembling those in the Lower Bracklesham Beds, including *W.* (*A.*) *homomorpha*, *W.* (*W.*) *articulata*, and *W.* (*W.*) *coleothrypta*. In the Argile d'Asse (Bartonian), Rozen (1965) recorded *W.* (*W.*) *clathrata* and *W.* (*W.*) *clathrata* subsp. *fasciata*, this latter appears to be, according to the illustrations, similar to *W.* (*W.*) aff. *articulata* recorded in the Upper Bracklesham Beds and Lower Barton Clays of south-east England. Weyns (1970) described the microplankton assemblages from the Sables de Grimmertingen (Tongrian) which include *W.* (*W.*) *articulata*, *W.* (*R.*) *draco*, and *W.* (*W.*) *varielongituda*. The specimen of *W.* (*R.*) *draco* figured by this author appears to have a perforated periphragm and could belong to *W.* (*R.*) *perforata*. The specimen figured as *W.* (*W.*) *varielongituda* does not correspond to this species and appears to belong to *W.* (*W.*) *symmetrica* or a related species. Two samples from the Rupel Clay were also available for the present work, they contain *W.* (*W.*) *articulata*, *W.* (*W.*) *ovalis*, *W.* (*W.*) *symmetrica*, and *W.* (*W.*) *gochtii* n. sp.



TEXT-FIG. 2. The range of selected *Wetzeliella* spp. in Belgium.

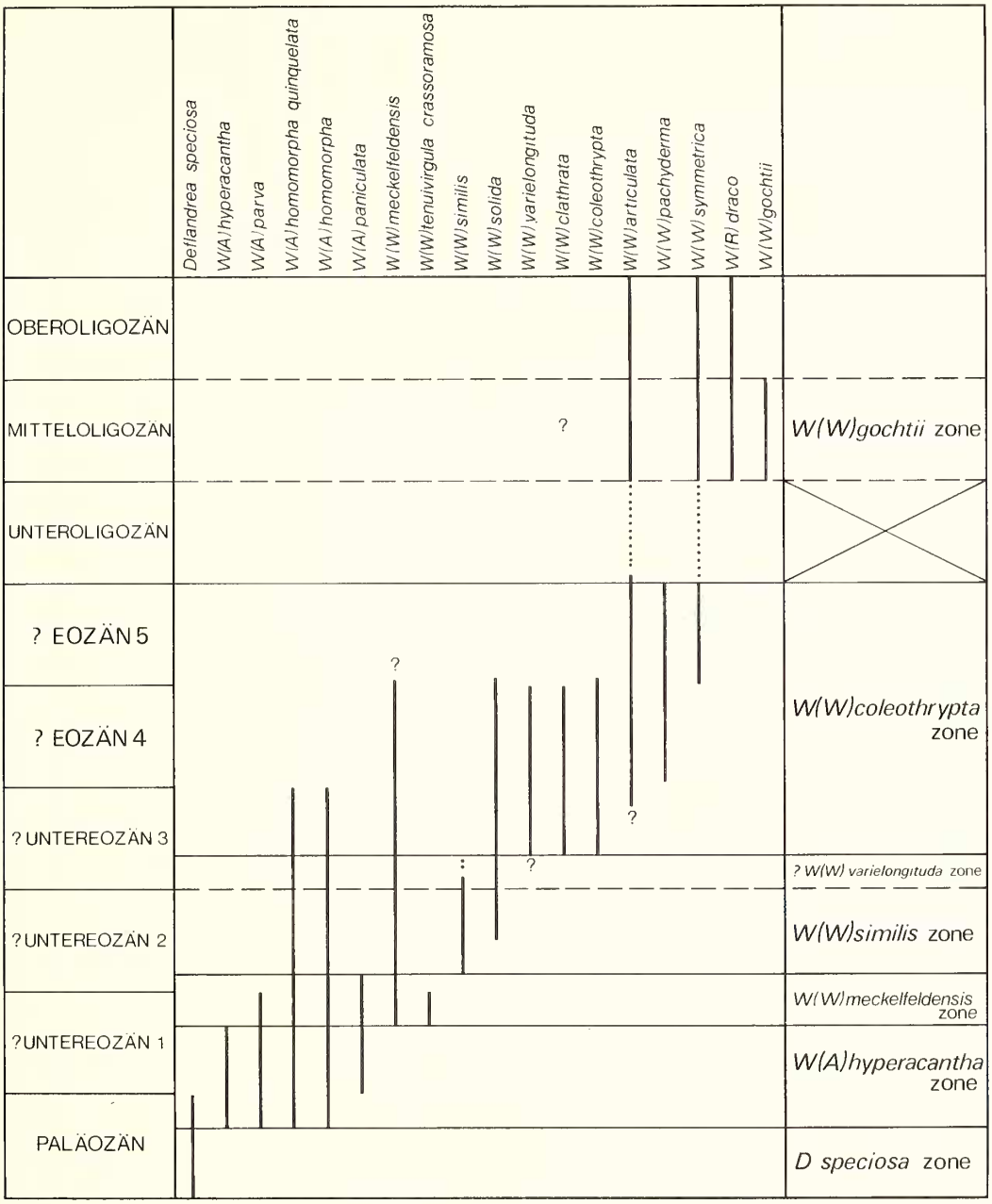
THE DISTRIBUTION OF *WETZELIELLA* IN NORTH GERMANY

The evidence provided by Morgenroth (1966), Agelopoulos (1967), and Gocht (1969), combined with the examination of the samples made available from Meckelfeld, give a fairly complete picture of the distribution of *Wetzeliella* in the Upper Palaeocene to Upper Eocene of north Germany. The information on the distribution of this genus in the Oligocene of north Germany has been taken from Eisenack (1938, 1954, 1965), Gocht (1955), Klumpp (1953), Weiler (1956), Maier (1959), Alberti (1961), Gerlach (1961), Brosius (1963), and Benedek (1972). Although the stratigraphical order of the Meckelfeld samples examined is known, their position relative to the German stages names is uncertain. These stages, however, have been established by Gocht (1969) in two borehole sections from the same locality. In constructing the table for text-fig. 3, an extrapolation has been made from these three sections. The scheme figured, consequently, should be regarded as provisional and the position of the stage boundaries may be modified as further information is made available.

The history of the genus *Wetzeliella* in north Germany appears to be, at least in general terms, the same as in the areas so far discussed. The succession of *Wetzeliella* species in the late Upper Palaeocene and Lower Eocene coincides with that observed in Belgium and south-east England. There are, however, some differences in the composition of the assemblages of the late Lower Eocene to Upper Eocene, part of which have already been pointed out by Morgenroth (1966). *W.* (*W.*) *coleothrypta* is rare or absent in assemblages corresponding to the Middle to Upper Eocene. *W.* (*R.*) *glabra*, which occurs both in England and in Belgium, is apparently absent in north Germany, where *W.* (*W.*) *samlandica* and *W.* (*W.*) *pachyderma*, not recorded in the areas treated above, are common. *W.* (*R.*) *draco* is apparently not present in the German stages attributed to the Upper Eocene, but the species is well known from Oligocene assemblages. *W.* (*R.*) *perforata* has not yet been recorded in north Germany. Oligocene dinoflagellate assemblages from north Germany include *W.* (*W.*) *articulata*, *W.* (*W.*) *ovalis*, *W.* (*W.*) *symmetrica*, *W.* (*W.*) *gochtii*, and *W.* (*R.*) *draco*. Maier (1959) has recorded *W.* (*W.*) *symmetrica* in deposits attributed to the Miocene.

WETZELIELLA ZONES IN NORTH-WEST EUROPE

The marked similarities observed in the distribution of *Wetzeliella* species in England, Belgium, and north Germany (area named here as north-west Europe), particularly in the late Upper Palaeocene and Lower Eocene, enables the genus to be applied to correlation and zonation within this area. A number of consecutive-range biozones based on first appearances of species of *Wetzeliella* can be distinguished, their position being apparently common to all areas under discussion. The succession of species in the Upper Eocene–Oligocene is not so clear. There are apparently some differences between England and Germany, such as the considerably earlier appearance of *W.* (*R.*) *draco* in the former and the absence of *W.* (*R.*) *perforata* in the latter. The evidence from Belgium is scant. Part of the differences observed may probably be due to stratigraphic gaps occurring in all three areas, and part also to gaps in the observation. Nevertheless, the evidence is enough to support the proposal of at least



TEXT-FIG. 3. The range of selected *Wetzeliella* spp. in north Germany.

a provisional scheme for the upper part of the Palaeogene, although the boundaries of the *Wetzeliella* zones have not been precisely determined. It should be noted that only the first occurrences of taxa have been taken into account in constructing the present scheme, as they are taken to be more reliable than the extinction of species. The disappearance of certain species may, however, be employed as additional features of the present zonation (e.g. the extinction of *W.* (*A.*) *hyperacantha* and *W.* (*A.*) *parva*, or the disappearance of a number of species in the Middle Eocene).

1. *Wetzeliella* (*Apectodinium*) *hyperacantha* Zone. Interval from the first appearance of the subgenus *Wetzeliella* (*Apectodinium*) to the first occurrence of *W.* (*Wetzeliella*) *meckelfeldensis*. Common *Wetzeliella* species: *W.* (*A.*) *parva*, *W.* (*A.*) *hyperacantha*, *W.* (*A.*) *homomorpha* subsp. *homomorpha*, *W.* (*A.*) *homomorpha* subsp. *quinquelata*, *W.* (*A.*) *paniculata*.

Distribution. England: Woolwich Beds at Charlton Brickpit, Erith and Upnor. Base of the London Clay at Whitecliff Bay and Herne Bay. Belgium: Sables d'Ostende-ter-Streep (Upper Landenian), Kallo. Germany: upper part of the Paläozän, Untereozän 1, Meckelfeld.

Remarks. Although *W.* (*A.*) *hyperacantha* is relatively rare in most of these assemblages, the name of the zone has been chosen to conform with the nomenclature introduced by Caro (1973).

2. *Wetzeliella* (*Wetzeliella*) *meckelfeldensis* Zone. Interval from the first occurrence of *W.* (*W.*) *meckelfeldensis* to the first appearance of *W.* (*W.*) *similis*. Common *Wetzeliella* species: *W.* (*W.*) *meckelfeldensis*, *W.* (*W.*) *tenuivirgula* subsp. *crassoramosa*, *W.* (*A.*) *paniculata*, *W.* (*A.*) *homomorpha* subsp. *homomorpha*, *W.* (*A.*) *homomorpha* subsp. *quinquelata*.

Distribution. England: London Clay at Herne Bay (5–18 m above the base), Whitecliff Bay, Alum Bay, and Studland Bay. Belgium: Argile d'Ypres (377–357 m), Kallo. Germany: top of Untereozän 1, lower part of Untereozän 2, Meckelfeld.

3. *Wetzeliella* (*Wetzeliella*) *similis* Zone. Interval from the appearance of *W.* (*W.*) *similis* to the first occurrence of *W.* (*W.*) *varielongituda*. Common *Wetzeliella* species: *W.* (*W.*) *similis*, *W.* (*W.*) *solida*, *W.* (*W.*) *meckelfeldensis*, *W.* (*A.*) *homomorpha* subsp. *homomorpha*, *W.* (*A.*) *homomorpha* subsp. *quinquelata*.

Distribution. England: London Clay at Whitecliff Bay (41–71 m above the base), Alum Bay, and Herne Bay. Belgium: Argile d'Ypres (357–305 m), Kallo. Germany: part of the Untereozän 2, Meckelfeld.

4. *Wetzeliella* (*Wetzeliella*) *varielongituda* Zone. Interval from the first appearance of *W.* (*W.*) *varielongituda* to the appearance of *W.* (*W.*) *coleothrypta*. Common *Wetzeliella* species: *W.* (*W.*) *varielongituda*, *W.* (*W.*) *solida*, *W.* (*W.*) *lunaris*, *W.* (*W.*) *clathrata*, *W.* (*W.*) *edwardsi*, *W.* (*W.*) *meckelfeldensis*, *W.* (*A.*) *homomorpha* subsp. *homomorpha*, *W.* (*A.*) *homomorpha* subsp. *quinquelata*.

Distribution. England: London Clay at Allhallows (Kent) and at Whitecliff Bay. Belgium: Argile d'Ypres (305–266 m), Kallo. Germany: ?lower part of the Untereozän 3, Meckelfeld.

5. *Wetzeliella* (*Wetzeliella*) *coleothrypta* Zone. Interval from the first occurrence of *W.* (*W.*) *coleothrypta* to the first appearance of *W.* (*Rhombodinium*) *draco*. Common *Wetzeliella* species: *W.* (*W.*) *coleothrypta*, *W.* (*W.*) *articulata*, *W.* (*W.*) *tenuivirgula*, *W.* (*W.*) *reticulata*, *W.* (*W.*) *clathrata*, *W.* (*W.*) *solida*, *W.* (*W.*) *varielongituda*, *W.* (*W.*) *condylos*, *W.* (*W.*) *pachyderma*, *W.* (*W.*) *samlandica*, *W.* (*R.*) *glabra*, *W.* (*W.*) *meckelfeldensis*, *W.* (*A.*) *homomorpha* subsp. *homomorpha*, *W.* (*A.*) *homomorpha* subsp. *quinquelata*, *W.* (*W.*) aff. *articulata*.

Distribution. England: London Clay, 36 m below the top at Sheppey. Bracklesham Beds at Whitecliff Bay and Alum Bay. Bournemouth Marine Beds. Hengistbury Head Beds (below the *Nummulites prestwichianus* Bed). Belgium: Argile d'Ypres (above 266 m), Kallo; also at Sint Jan, Tielt, and Merelbeke. Paniselian (P1). Argile d'Asse. Germany: upper part of the Untereozän 3, Untereozän 4, and Eozän 5 (Oberes Eozän), Meckelfeld. Eozän 4 and Obereozän, Holstein.

Remarks. This extensive zone can be subdivided on two bases, the extinction of some *Wetzeliella* species and the range of varieties of *W.* (*W.*) *articulata*. A subzone is clearly defined in England at the top of the

Bracklesham Beds (Fisher's Beds XIV–XIX) by the occurrence of *W.* (*W.*) aff. *articulata*; this subzone appears to be also recognizable in the Argile d'Asse (Belgium), but not so in north Germany. The top of this zone has not been located in Germany, but it apparently corresponds to the top of the Eozän 5 (Oberes Eozän).

6. *Wetzeliella* (*Rhombodinium*) *draco* Zone. Interval from the appearance of *W.* (*R.*) *draco* to the appearance of *W.* (*R.*) *perforata*. Common *Wetzeliella* species: *W.* (*R.*) *draco*, *W.* (*W.*) *articulata*, *W.* (*W.*) aff. *articulata*, *W.* (*W.*) *coleothrypta*, *W.* (*A.*) *homomorpha* subsp. *homomorpha*.

Distribution. England: Lower Barton Clays at Alum Bay (base to 36 m), Whitecliff Bay, Highcliffe. Hengistbury Head Beds (above the *Nummulites prestwichianus* Bed) at Hengistbury Head.

Remarks. This zone cannot be established either in Belgium or in Germany due, apparently, to the existence of stratigraphic discontinuities where the present zone should occur. *W.* (*R.*) *draco* is known to occur in the Upper Eocene of off-shore Atlantic Canada (Williams 1975) but in north Germany and Belgium it has only been recorded in the Oligocene.

7. *Wetzeliella* (*Rhombodinium*) *perforata* Zone. Interval from the first occurrence of *W.* (*R.*) *perforata* to the first appearance of *W.* (*W.*) *gochtii* n. sp. Common *Wetzeliella* species: *W.* (*R.*) *perforata*, *W.* (*R.*) *draco*, *W.* (*R.*) *longimanum*, *W.* (*W.*) *articulata*, *W.* (*W.*) *coleothrypta*, *W.* (*W.*) *symmetrica*, *W.* (*A.*) *homomorpha* subsp. *homomorpha*.

Distribution. England: the base of this zone lies 36 m above the base of the Barton Clays at Highcliffe; the upper part is represented by the Middle Headon Beds at Whitecliff Bay. Belgium: ?Sables de Grimmertingen (Tongrian).

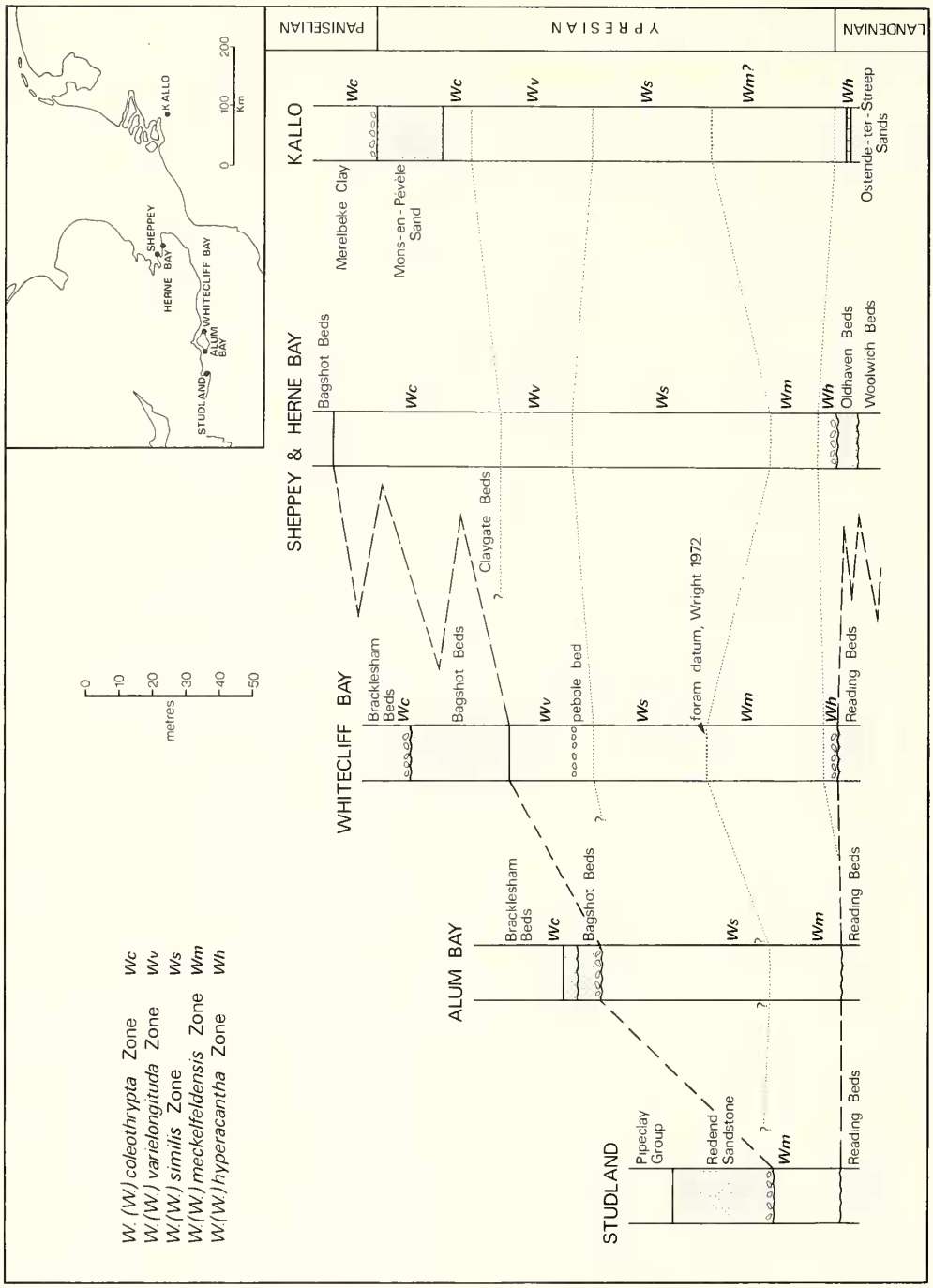
8. *Wetzeliella* (*Wetzeliella*) *gochtii* Zone. The base of this zone is at the first appearance of *W.* (*W.*) *gochtii*. Its position cannot be accurately established in the English succession because of unfavourable environments between the Middle Headon Beds and the Upper Hamstead Beds. The zone is recorded from the Upper Hamstead Beds of the Isle of Wight, from the Rupel Clay in Belgium, and from the Lintforten Schichten of Germany (Benedek 1972). Common *Wetzeliella* species: *W.* (*W.*) *gochtii*, *W.* (*W.*) *symmetrica*, *W.* (*W.*) *articulata*, *W.* (*W.*) *ovalis*, *W.* (*R.*) *draco*.

Remarks. This zone should be considered tentative until fuller examination of the Belgian and German sequences has been carried out.

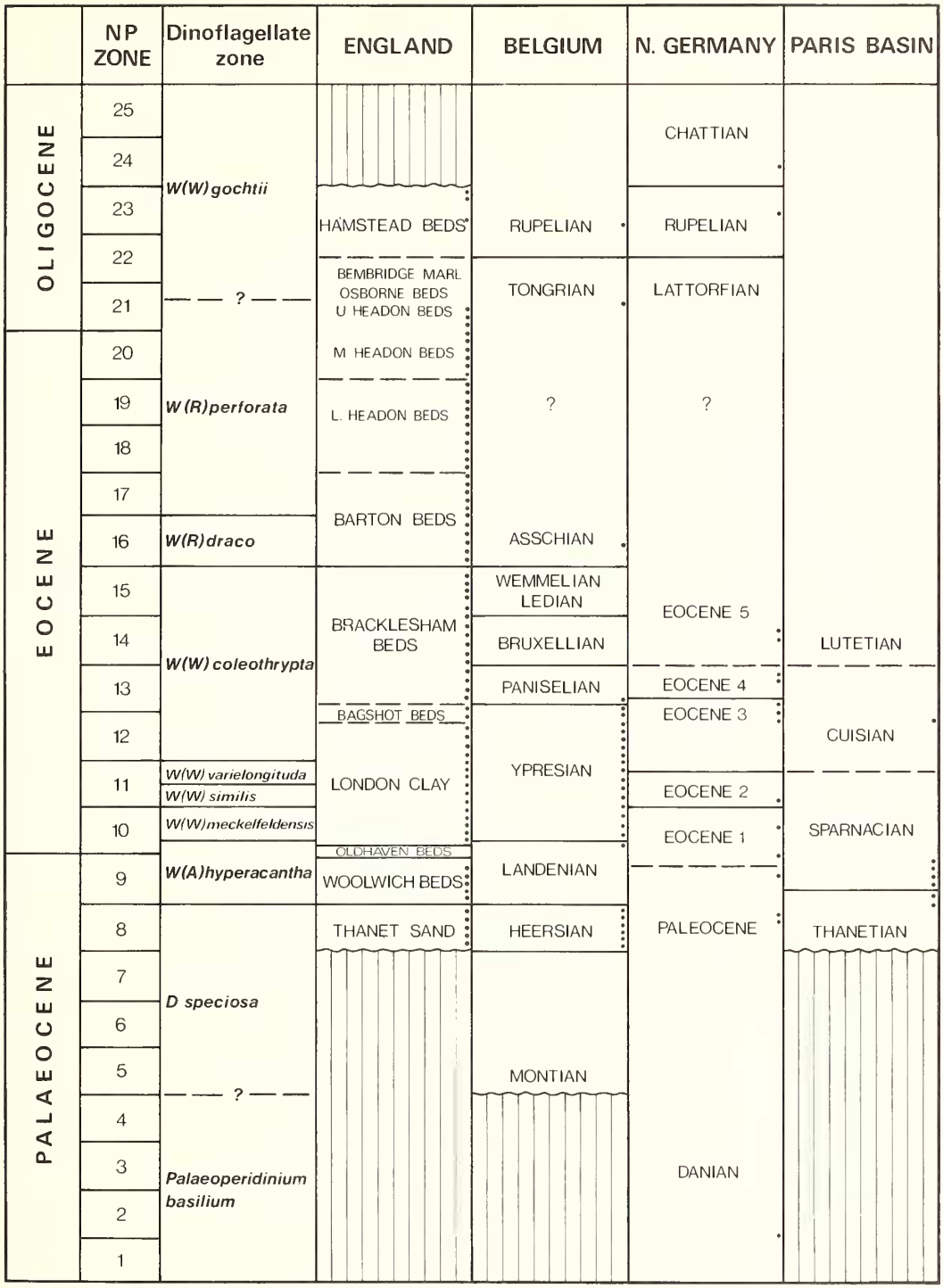
CORRELATION BASED ON *WETZELIELLA* IN NORTH-WEST EUROPE

The application of the zonation based on *Wetzeliella* can be extended from the western part of the Hampshire Basin to Belgium and north Germany and is particularly effective in the Upper Palaeocene and Lower Eocene.

The first appearance of *Wetzeliella* is a valuable datum recognizable in several European localities in and outside the present area. The *W.* (*A.*) *hyperacantha* Zone allows correlation of the Woolwich Beds with the Landenian, the Lower Sparnacian, and the upper part of the German Paläozän (text-fig. 5). The top of the *W.* (*A.*) *hyperacantha* Zone lies in the basal few metres of the London Clay at Herne Bay and Whitecliff Bay. The top of this zone has not been located at Alum Bay, but it may lie at the base of the London Clay. De Coninck (1968) shows the incoming of *W.* (*W.*) *nieckelfeldensis* 2·85 m above the base of the Argile D'Ypres and the occurrence of *W.* (*A.*) *parva* up to this point; in his later work (1972) the main change is indicated at the base of the clay and *W.* (*A.*) *parva* restricted to the Landenian. The top of the present zone therefore either coincides with the Landenian/Ypresian boundary or lies about 3 m higher. In any case, the London/Ypres Clay transgression appears to be very rapid, if not simultaneous, over the whole area, only a slight overlap is



TEXT-FIG. 4. Correlation of the London Clay and Argile d'Ypres based on *Wetzeliella* spp. Dashed lines, lithological boundaries; dotted lines, palaeontological boundaries.



TEXT-FIG. 5. General correlation in north-west Europe based on nannoplankton and dinoflagellates. Dots indicate approximate position of dinoflagellate assemblages.

possible on the west of the Hampshire Basin. The top of this zone in north Germany lies in the Eozän 1, presumably near the top of this stage. This zone can also be extended to the Paris Basin, where it occurs in the Sables de Bracheux (Thanetian II, Zone 1 of Chateauneuf and Gruas-Cavagnetto 1968). The *W.* (*A.*) *hyperacantha* Zone has also been widely recognized in the North Sea Basin.

The *W.* (*W.*) *meckelfeldensis* Zone appears to be 15–30 m thick in the London/Ypres Clay Basin. In the London Clay, its top coincides with the boundary between lower and upper dinoflagellate assemblages recognized by Williams (1963) and also with the position of the planktonic foraminifera datum of Wright (1972) at Whitecliff Bay. At Studland, the zone was recognized in a sample from within 2 m below the top of the London Clay. A considerable non-sequence is therefore present at Studland Bay which diminishes eastwards. At Alum Bay its position is uncertain because of the absence of critical species but this non-sequence most likely lies above the *W.* (*W.*) *similis* Zone. At Whitecliff Bay, the sands appear below the *W.* (*W.*) *coleothrypta* Zone while at Sheppey about 35 m of clay belonging to the *W.* (*W.*) *coleothrypta* Zone intervene before the onset of the Bagshot Sands. Thus, the regression appears to have started at about the beginning of the *W.* (*W.*) *coleothrypta* Zone, and this was accompanied by uplift and erosion to the west. The Mons-en-Pévèle Sands, near the base of the *W.* (*W.*) *coleothrypta* Zone in Belgium, appear to be somewhat younger than the Bagshot Sands. The Mons-en-Pévèle Sands differ from the Bagshot Sands in their being marine in character, glauconitic and with abundant dinoflagellates, coccoliths, and foraminifera, and they presumably have a source to the east, in contrast to the barren (?fluvial) Bagshot Sands with a source to the west and north-west.

The *W.* (*W.*) *varielongituda* Zone is 25–45 m thick in the London/Ypres Clay Basin, its top is found about 35 m below the Bagshot Sands in the section exposed at Sheppey and a short distance below the Mons-en-Pévèle Sands at Kallo. This zone has not been clearly identified in north Germany; although *W.* (*W.*) *varielongituda* is abundant in some horizons, it is already associated with *W.* (*W.*) *coleothrypta* and presumably the *W.* (*W.*) *varielongituda* Zone should lie below these horizons, probably in the lower part of the Untereozän 3.

The *W.* (*W.*) *coleothrypta* Zone extends through a thick succession including not only the upper 35 m or so of the London Clay at Sheppey but also the whole of the Bracklesham Beds. This zone embraces the calcareous nannoplankton zones 12–15 of Martini (1971) and covers a number of dinoflagellate zones established by Eaton (1971) for the Bracklesham Beds. The present zone is recognizable in the uppermost few metres of the Argile d'Ypres, the Mons-en-Pévèle Sands, and the Merelbeke Clay. It is also found in the Eozän 3, 4, and 5 of Germany. The Røsnaes Clay of Denmark (Caro 1973; Caro *et al.* 1975) may either belong to this zone or lie as early as the *W.* (*W.*) *similis* Zone. The position is not clear from the available information, but the occurrence of *W.* (*W.*) *pachyderma* (present also in the Untereozän 4 and Eozän 5 of north Germany) and *W.* (*W.*) *clathrata* suggests the presence of the *W.* (*W.*) *coleothrypta* Zone.

The *W.* (*R.*) *draco* Zone occupies only the lower part of the Barton Clay, its base being located immediately above the *Nummulites prestwichianus* Bed. This zone has not been recognized outside England, although the Argile d'Asse in Belgium might

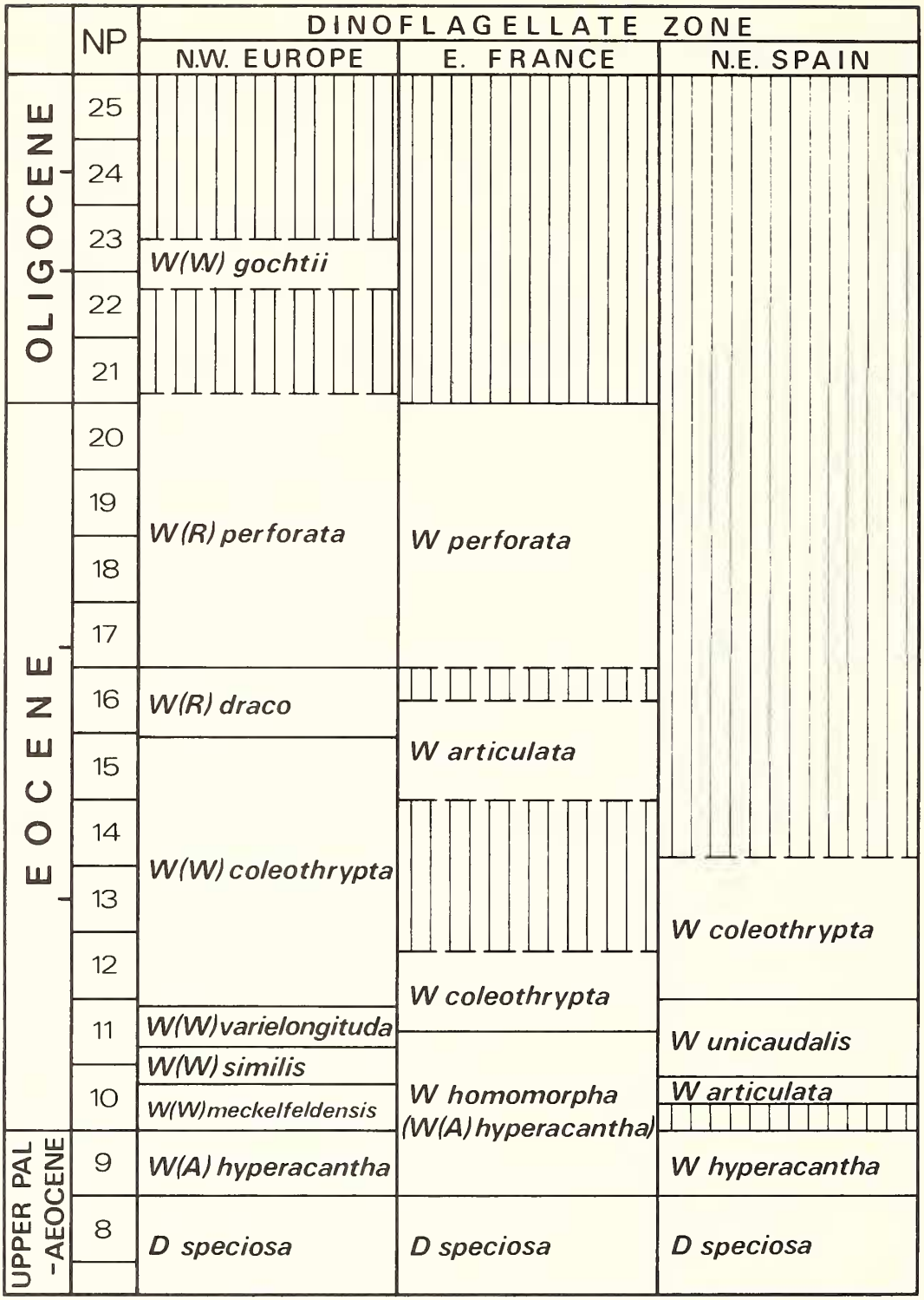
be its equivalent. The *W.* (*R.*) *perforata* Zone begins in the Middle Barton Clay and extends up to the top of this sequence; it has also been recognized in the Middle Headon Beds. The Sables de Grimmertingen (Tongrian) which contain forms resembling *W.* (*R.*) *perforata* may belong to this zone. The *W.* (*R.*) *perforata* Zone has not been recognized in north Germany.

The highest zone, that of *W.* (*W.*) *gochtii*, is found in the Upper Hamstead Beds. The base of this zone has not been located since the intervening Upper Headon Beds, Osborne Beds, Bembridge Beds, and Lower Hamstead Beds are for the most part non-marine (Liengjarern, unpublished thesis, Sheffield 1973) and contain very few dinoflagellates. The *W.* (*W.*) *gochtii* Zone occurs in the Argile de Rupel in Belgium and also in the Lintforter Schichten (Rupelian) of Tönisberg in north Germany. Above the Middle Oligocene in western Europe, *Wetzeliella* is restricted to very few species (*W.* (*W.*) *symmetrica*, *W.* (*W.*) *articulata*, and *W.* (*R.*) *draco*) and the genus appears to be of little value in correlation.

WETZELIELLA IN OTHER WEST EUROPEAN AREAS

So far the discussion has been restricted to the distribution and stratigraphic application of *Wetzeliella* in north-west Europe (south-east England, Belgium, and north Germany), but a large number of the *Wetzeliella* species present in this area are also well known from other European localities. As mentioned earlier, *Wetzeliella* has already been employed in the construction of biostratigraphical schemes in the Palaeocene–Lower Eocene of the southern Pyrénées in north-east Spain (Caro 1973; Caro *et al.* 1975), the Alpine flysch in east France (Jan du Chêne *et al.* 1975) as well as in the Palaeogene of the Ukraine and Crimea (Grigorovich 1969, 1971). There are also a number of records from the Palaeocene–Eocene of France (Chateauneuf and Gruas-Cavagnetto 1968; Gruas-Cavagnetto 1968, 1970), the Priabonian of north Italy (Gruas-Cavagnetto 1974), the Eocene of Romania (Baltes 1969), and several deposits in the U.S.S.R. (Eisenack 1938, 1954; Alberti 1961; Vozzhennikova 1967; Olyenik 1973; Aristova 1973; Grigorovich and Vyesyelov 1973).

As shown on text-fig. 5, a correspondence can be established between the *Wetzeliella* zones in north-west Europe and Martini's standard zonation based on calcareous nannoplankton (1971), and correlation based on *Wetzeliella* agrees with that founded on calcareous nannoplankton. This provides a reliable stratigraphic reference that can be applied to correlate the *Wetzeliella* zones recognized for north-west Europe with those defined for the southern Pyrénées and the French Alps (text-fig. 6). The lowest dinoflagellate zone on text-fig. 6, the *Deflandrea speciosa* Zone, has been recognized (although its range is not established precisely) in England, Belgium, and north Germany immediately below the first occurrence of *Wetzeliella*. The *W.* (*A.*) *hyperacantha* Zone is common to all areas under consideration, its base, which in fact marks the beginning of the known history of *Wetzeliella*, can be regarded as an important stratigraphic datum which can be identified not only in the areas shown on text-fig. 6, but also in Greenland, the North Sea Basin, north France, and the U.S.S.R. and possibly also as far as Australia and New Zealand. The north-west European *W.* (*W.*) *meckelfeldensis*, *W.* (*W.*) *similis*, and *W.* (*W.*) *varielongituda* zones have not been identified in other European areas, and there is no information



TEXT-FIG. 6. Comparison of the *Wetzeliella* zonal scheme for north-west Europe with those for the Pyrénées and the western Alps.

available about the distribution of the key species in deposits outside north-west Europe, although these species are known to occur in other localities. In zoning the section at Campo (southern Pyrénées), Caro (1973) leaves a gap in the scheme above the top of the *W.* (*A.*) *hyperacantha* Zone, this may be the equivalent of part of the missing boreal zones. Caro's *W. articulata* Zone corresponds to the nannoplankton zone NP 10. Typical *W.* (*W.*) *articulata*, however, does not seem to appear in north-west Europe at least until the NP Zone 11. Some possible precursors of this species, some of which were classified as *W.* (*W.*) *lunaris* by Gocht (1969), do occur as early as the *W.* (*W.*) *similis* Zone. The *W. unicaudalis* Zone of north-east Spain probably is the equivalent of the boreal *W.* (*W.*) *varielongituda* Zone and part of the *W.* (*W.*) *coleothrypta* Zone; *W. unicaudalis* has so far only been recorded in its type locality and no similar forms have been observed in north-west Europe. Caro's *W. coleothrypta* Zone, at the top of the section at Campo, most likely corresponds to the lower part of the zone established in north-west Europe on the same species.

In the Grés de Voirons (Alpine flysch), *W.* (*A.*) *hyperacantha* occurs in the lower part of the *W. homomorpha* Association established by Jan du Chêne *et al.* (1975), this part of the section corresponds to the *W.* (*A.*) *hyperacantha* Zone recognizable in all other areas. The *W. homomorpha* Association in the Alpine flysch extends up to the appearance of *W.* (*W.*) *coleothrypta* (in the NP Zone 11), i.e. it is equivalent to the north-west European *W.* (*W.*) *meckelfeldensis*, *W.* (*W.*) *similis*, and *W.* (*W.*) *varielongituda* zones. It should be noted that in some more northerly Lower Eocene sections, such as the London Clay at Alum Bay, neither the *W.* (*W.*) *similis* Zone nor the *W.* (*W.*) *varielongituda* Zone have been precisely established due to the fact that in most beds throughout the section the only species of *Wetzeliella* present is *W.* (*A.*) *homomorpha*. It appears that *W.* (*A.*) *homomorpha* favours environments in which other *Wetzeliella* species are rare or do not occur at all, in the case of the London Clay at Alum Bay possibly because of lower salinities in a near-shore environment as suggested by Downie *et al.* (1971). The absence of the critical *Wetzeliella* species in the Alpine flysch might also be due to environmental conditions. The *W.* (*W.*) *coleothrypta* Zone has also been established in the Grés de Voirons, its base is apparently contemporaneous with the base of the zone in north-west Europe, according to the nannoplankton zonal scheme. The top of this zone in the flysch is unknown since the section is interrupted by a stratigraphical discontinuity.

The next zone defined in the Alpine flysch is the *W. articulata* Association, of which neither the base nor the top have been established because of stratigraphical gaps. This zone, defined by Jan du Chêne *et al.* (1975) as equivalent to the NP Zone 15 or older, apparently corresponds to the upper part of the *W.* (*W.*) *coleothrypta* Zone in north-west Europe. The *W. perforata* Association of Jan du Chêne *et al.* ranges from the NP Zone 16 to the top of the NP Zone 20, which agrees with the distribution of the zone based on the same species in the south-east of England. *W.* (*R.*) *draco*, which in England appears below the *W.* (*R.*) *perforata* Zone apparently does not occur in the Alpine flysch until the Oligocene (Jan du Chêne, pers. comm.).

SYSTEMATIC PALAEONTOLOGY

Division PYRRHOPHYTA
Class DINOPHYCEAE Fritsch, 1935
Order PERIDINIALES Haeckel, 1894
Family DEFLANDREACEAE Eisenack, 1954, emend. Sarjeant and Downie 1974
Genus *Wetzeliella* Eisenack, 1938, emend. Williams and Downie 1966
Subgenus *Wetzeliella* (*Apectodinium*) subgen. nov.

Derivation of name. Greek, 'apektos', uncombed.

Type species. Wetzeliella (*Apectodinium*) *homomorpha* Deflandre and Cookson 1955; p. 254, pl. 5, fig. 7.

Diagnosis. A subgenus of the genus *Wetzeliella* with pericoel absent or confined to small areas at the base of the horns. At the archeopyle margins the periphragm and endophragm are in close contact when both walls are observable. The processes are randomly distributed over the test surface or some can be roughly arranged along part of sutural lines.

Remarks. The species in this subgenus are in general considerably smaller in size than the other *Wetzeliella* species. The endophragm, which may be absent, is very thin, usually difficult to observe, and in close contact with the periphragm over most of the surface, separating only, if at all, at the base of the horns. Deformations of the endophragm which do not affect the periphragm are observable in many specimens showing that the walls are, in fact, separate. However, in contrast to what occurs in other *Wetzeliella* subgenera, the two layers remain attached in the opercula and around the apertures of the archeopyle, so that the shape of the aperture is the same on both the periphragm and the endophragm.

The species in this subgenus are distinguished by the shape and size of the horns, but there are abundant intermediate forms between them so that specific determinations may be on occasions somewhat arbitrary.

The subgenus *Wetzeliella* (*Apectodinium*) resembles *Spinidinium* and some spinose species of *Deflandrea* (e.g. *D. echinoidea*, *D. macmurdoensis*, etc.) in the size, structure of the walls, absence of lateral horns in many forms, shape of the archeopyle, and distribution of the ornament, but it differs in the shape of the ornament. In *Spinidinium*, and similarly ornamented species of *Deflandrea*, the ornament consists of short rods or spines, solid or hollow and closed distally; on the other hand, *Wetzeliella* (*Apectodinium*) bears long hollow processes, simple or bifurcate, and usually open distally. This subgenus is taken to represent or be related to the original stock from which most other *Wetzeliella* species derived; its main characters, i.e. small size, poorly differentiated endoblast, absence of lateral horns in many forms, variability in the development of the horns, abundant processes randomly arranged or crudely in part along sutures, etc., are regarded as primitive for the genus *Wetzeliella*.

Wetzeliella (*Apectodinium*) *paniculata* sp. nov.

Plate 92, fig. 1

?1969 *Wetzeliella* sp. 1; Gocht; p. 21, pl. 10, fig. 8; text-fig. 14.
1973 *Wetzeliella* sp.; Caro; p. 368, pl. 5, fig. 3.

Derivation of name. Latin, 'paniculus', small tuft.

Diagnosis. A species of *Wetzeliella* (*Apectodinium*) with a broadly rounded to subtriangular epitract and a subpolygonal hypotract. Apical horn absent or very much reduced; lateral horns broad and commonly long; well-developed antapical horns with a broad proximal part usually projecting into a long and complexly branched process.

Type locality. London Clay (Lower Eocene), Alum Bay, Isle of Wight, England.

Holotype. R. 36/4, slide ML 1193, rep. Micropalaeontology Laboratory, Department of Geology, University of Sheffield.

Dimensions. Holotype: over-all tract length 81 μ, breadth 92 μ; endoblast length 66 μ, breadth 74 μ; apical horn 3 μ; lateral horns 15 μ; antapical horn right 17 μ, left 15 μ; processes length 5–17 μ. Observed range: over-all length 93–76 μ, breadth 95–76 μ; apical horn 0–4 μ; lateral horns 9–18 μ; antapical horns 11–20 μ; processes length 5–18 μ. Number of specimens measured: ten.

Description. The apical horn is absent or, if present, reduced to a short, blunt projection surmounted by a tuft of processes; the epitract is broadly rounded to subtriangular in outline. The lateral horns are variable in length and they may be reduced, but they are typically long, rather broad, sometimes bifurcating distally, and abundantly covered by processes. The antapical horns consist of a broad and usually short proximal part and a long, branched distal process; the proximal part of the antapical horns may be very short, the horns then being reduced to the long ramified process. Both antapical horns are of roughly the same length. The endophragm, which may be absent in some specimens, is frequently very thin and difficult to observe. The processes are long, intratabular, with sometimes tapering bases and long tubiform distal parts which may be simple, bifurcate or, at the antapical horns, complexly branched. The processes are commonly open distally, the distal margin bearing a variable number of very short aculei, but they may also be closed with simple or bifid distal endings. The archeopyle is of the type common to the subgenus, i.e. small, subquadrangular, with periphragm and endophragm in close contact at the margins.

Remarks. The present species resembles *W.* (*A.*) *homomorpha* subsp. *quinquelata*, from which it differs by the long lateral horns; there are, however, numerous transitional forms between these taxa. *W.* (*A.*) *paniculata* differs from *W.* (*A.*) *hyperacantha* mainly in the absence of a well-developed apical horn and in the shape of the antapical horns; these in *W.* (*A.*) *hyperacantha* are shorter and do not bear a long ramified process distally. Other species in the subgenus *Wetzeliella* (*Apectodinium*) are: *W. parva* Alberti, 1961, *Palaeontographica*, **A 116,** p. 8, pl. 1, figs. 14–18; *W. hyperacantha* Cookson and Eisenack, 1965, *Proc. Roy. Soc. Victoria*, **79,** pp. 134–135, pl. 16, figs. 3–6.

Subgenus *Wetzeliella* (*Wetzeliella*) Eisenack, 1938, emend. Williams and Downie 1966

Wetzeliella (*Wetzeliella*) *gochtii* sp. nov.

Plate 92, figs. 2–3

1972 *Wetzeliella* (*Wetzeliella*) *symmetrica* Weiler var.; Benedek; p. 17, pl. 3, fig. 10*a*, *b*.

Derivation of name. This species has been named after Dr. Hans Gocht.

Diagnosis. A species of *Wetzeliella* (*Wetzeliella*) with usually subpentagonal tests.

Endoblast following closely the periblast outline but leaving a narrow and well-defined pericoel. All horns reduced to short, blunt projections or absent. The right antapical horn, when present, is markedly shorter than the left antapical horn. Abundant processes, variable in shape, usually rather flexible, open or closed distally.

Type locality. Rupel Clay (Middle Oligocene), 30 m above base, Belgium.

Holotype. T 36/2, slide ML 1194, rep. Micropalaeontology Laboratory, Department of Geology, University of Sheffield.

Dimensions. Holotype: over-all tract length 113 μ, breadth 108 μ; endoblast length 97 μ, breadth 93 μ; apical horn 0 μ; lateral horns 6 μ; antapical horn right 10 μ, left 5 μ; processes length 6–15 μ. Observed range: over-all length 118–107 μ, breadth 111–98 μ; apical horn 13–0 μ; lateral horns 10–4 μ; antapical horn right 12–5 μ, left 5–0 μ; processes length 5–18 μ. Number of specimens measured: six.

Description. Due to the variable development of the horns, the tracts may be subpentagonal, subrhombic, or subcircular, pentagonal outlines being dominant; in all cases the outline is rounded. The horns, when present, are very short, broad, and blunt. The endophragm lies close to the periphragm but there is always a well-defined, although narrow, pericoel, often continuous around the endoblast. The processes vary in shape and characters of the distal endings. Most commonly they are thin-walled, flexible, and frequently with tapering bases. They may be open or closed distally; when open, the distal margin is aculeate or entire, when closed, the distal ending is simple, acuminate, or capitate. In all the specimens observed the opercula are *in situ* and the archeopyle sutures are frequently difficult to observe.

Remarks. This species resembles *W.* (*W.*) *symmetrica* in the flexible, usually thin-walled processes, but differs from it by having all horns reduced or absent and a more rounded and commonly subpentagonal outline in contrast to the rhombic outlines with four well-developed horns characteristic of *W.* (*W.*) *symmetrica*. Some subcircular individuals of this species resemble *W.* (*A.*) *homomorpha*, from which they are distinguishable by the well-defined pericoel. *W.* (*W.*) *ovalis* also has reduced horns and rounded outlines, but its antapical horns are of about the same length and its processes are shorter, usually thicker-walled, and more rigid than in *W.* (*W.*) *gochtii*.

EXPLANATION OF PLATE 92

Fig. 1. *Wetzeliella* (*Apectodinium*) *paniculata* sp. nov. Holotype × 500.
Fig. 2. *Wetzeliella* (*Wetzeliella*) *gochtii* sp. nov. Holotype × 500.
Fig. 3. *Wetzeliella* (*Wetzeliella*) *gochtii* sp. nov. Specimen from the Hamstead Beds, Isle of Wight. × 500.
Fig. 4. *Wetzeliella* (*Wetzeliella*) sp. aff. *articulata* Eisenack. Bracklesham Beds, Hengistbury Head, Hampshire. × 500.
Fig. 5. *Wetzeliella* (*Rhombodinium*) *perforata* Jan du Chêne and Chateauneuf. Middle Headon Beds, Whitecliff Bay, Isle of Wight. × 500.
Fig. 6. *Wetzeliella* (*Apectodinium*) *hyperacantha* Cookson and Eisenack, Woolwich Beds, Bean, Kent. × 500.

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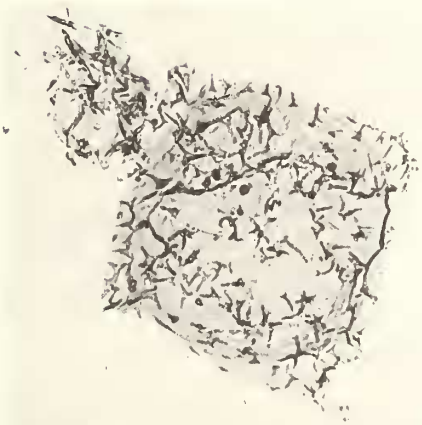

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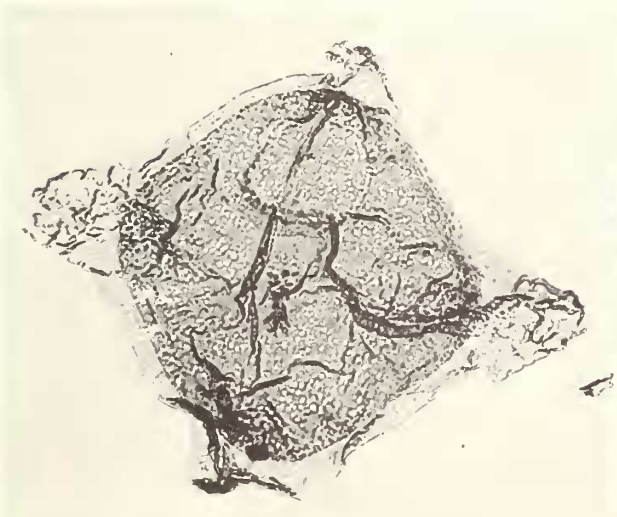

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6

COSTA and DOWNIE, *Wetzeliella*

Wetzeliella (*Wetzeliella*) aff. *articulata*

Plate 92, fig. 4

Remarks. These forms are smaller than *W.* (*W.*) *articulata*, with usually very thin walls and all horns reduced. The processes are also thin-walled and quite flexible, and their distal margins are very variable. These may be aculeate (the aculei sometimes uniting neighbouring processes), secate, or bear fragments of a distal reticulum or membrane. In all the specimens observed the operculum is *in situ* and the archeopyle sutures, when at all observable, are very faint. *W.* (*W.*) *articulata* is almost always present in the same assemblages where the present forms occur, as well as, sometimes, *W.* (*W.*) *coleothrypta* and *W.* (*W.*) *reticulata*; transitional forms to *W.* (*W.*) *articulata* are not uncommon. The characters of *W.* (*W.*) aff. *articulata*, particularly the fact that the archeopyle sutures are only faintly marked on the periphragm and are often incomplete, appear to suggest that these forms may be abnormally developed cysts of *W.* (*W.*) *articulata* or a related species.

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APPENDIX—LIST OF *WETZELIELLA* SPECIES

Subgenus *Wetzeliella* (*Apectodinium*) subgen. nov.

**W.* (*A.*) *homomorpha* subsp. *homomorpha* Deflandre and Cookson, 1955
W. (*A.*) *homomorpha* subsp. *quinquelata* (Williams and Downie, 1966)
W. (*A.*) *hyperacantha* Cookson and Eisenack, 1965
W. (*A.*) *paniculata* sp. nov.
W. (*A.*) *parva* Alberti, 1961

Subgenus *Wetzeliella* (*Wetzeliella*) Eisenack, 1938, emend. Williams and Downie, 1966

**W.* (*W.*) *articulata* Eisenack, 1938
W. (*W.*) *clathrata* Eisenack, 1938
W. (*W.*) *clathrata* subsp. *fasciata* (Rozen, 1965)
W. (*W.*) *coleothrypta* Williams and Downie, 1966
W. (*W.*) *condylos* Williams and Downie, 1966
W. (*W.*) *edwardsi* Wilson, 1967
W. (*W.*) *goclitii* sp. nov.
W. (*W.*) *lunaris* Gocht, 1969
W. (*W.*) *meckelfeldensis* Gocht, 1969
W. (*W.*) *ovalis* Eisenack, 1954
W. (*W.*) *pachyderma* Caro, 1973
W. (*W.*) *reticulata* Williams and Downie, 1966
W. (*W.*) *samlandica* Eisenack, 1954
W. (*W.*) *similis* Eisenack, 1954
W. (*W.*) *solida* (Gocht, 1955) Williams and Downie, 1966
W. (*W.*) *symmetrica* Weiler, 1956
W. (*W.*) *tenuivirgula* Williams and Downie, 1966
W. (*W.*) *tenuivirgula* subsp. *crassoramosa* (Williams and Downie, 1966)
W. (?*W.*) *unicaudalis* Caro, 1973
W. (*W.*) *varielongituda* Williams and Downie, 1966

Subgenus *Wetzeliella* (*Rhombodinium*) (Gocht, 1955) Alberti, 1961

**W.* (*R.*) *draco* (Gocht, 1955) Alberti, 1961
W. (*R.*) *glabra* Cookson, 1956
W. (*R.*) *longimanum* Vozzhennikova, 1967
W. (*R.*) *perforata* Jan du Chêne and Chateauneuf, 1975